TERRITORIAL BEHAVIOR IN SAVANNAH SPARROWS IN SOUTHEASTERN MICHIGAN

Peter E. Potter

The Savannah Sparrow (*Passerculus sandwichensis*) is a bird of open grasslands, bogs, coastal marshes, and tundra. In southeastern Michigan its thin insect-like song is heard wherever farming has produced pastures and fallow fields. It migrates south in late summer and fall and returns in April and early May. For three successive breeding seasons (1965–67) I observed the territorial behavior in Savannah Sparrows in a field five miles west of Ann Arbor, Washtenaw County, Michigan. The population ranged from about 18 pairs in 1965 to 12 pairs in 1967.

METHODS

The study area was measured off in a grid, with tape markers placed along border fences and metal ground markers at the grid intersections in the field. Song perches were marked with colored pipe cleaners, some with colored foam plastic balls attached. Adult birds were netted and marked with aluminum and color-coded plastic bands. Sex was determined by behavior since there is no discernible difference in appearance. Nestlings were marked only with aluminum bands. (Only one bird banded as a nestling later returned to the study field to breed.) Fifty-two adults were banded in 1965, 12 in 1966, and 6 in 1967, a total of 70. Seventy-five young were banded in 1965, 29 in 1966, and 26 in 1967, a total of 130. (Banding in 1966 and 1967 was more selective, aimed at birds evidently linked to a territory. In several instances, females on their nests were flushed into nets posted near them. Only one non-resident Savannah Sparrow was caught in each of those years, contrasted to 19 in 1965.)

I observed the birds mostly on Fridays and Sundays from 06:00 to 12:00. Occasionally, I made evening visits. In all, I spent 490 hours in observation.

Because Savannah Sparrows spend so much of their time on the ground, it was impossible to determine their territorial boundaries where vegetation was dense. "Walking" the birds around their territories was not feasible since they would leave their territories when pressed. Neither did many territories touch others, where the males might have clashed and revealed the borders. It was necessary, therefore, to fall back on the device of marking the males' singing perches to provide an approximation of the territorial areas. When singing was done on the ground, usually during pauses in foraging among the hummocks of grass, adjacent grass clumps or weed stalks were marked.

Gradually the accumulation of markers described areas the edges of which appeared to be defended consistently. Furthermore, the birds did not appear to go much beyond these markers to defend their territories. Thus, the variation between the edges of those areas described by markers and the actual territorial boundaries seemed slight enough to make the location of the territories clear and the measurement valid.

STUDY AREA

The study field contained 4.74 hectares (11.72 acres) and was essentially level and poorly drained. It was bounded on the south by a gravel road and a brushy field, to the north by cropland, and on either side by wet pastures.

Most of the study field was covered by bluegrass (*Poa pratensis*) fallen over or blown down in successive layers to form hummocks 30 to 50 centimeters in diameter and up to 30 centimeters high. The bluegrass and interspersed timothy (*Phleum pratensis*) grew up to 45 centimeters tall by mid-June. In widely separated locations were slowly-spreading circles of sedge (*Carex stipata*); chickweed (*Stellaria graminea*) was also prevalent.

The northern half of the field was free of woody plants except for a small copse of willows (*Salix sp.*) up to 4.5 meters tall at one place along the northern fence. The southern half contained scattered clumps of willow (*Salix petiolaris*) from one-half to two meters tall. The field had occasionally been used as pasture for cattle in previous years, including the year immediately preceding the study period, but no cattle were there during the study period itself. In those three years there was an increase in the amount of thistle (*Cirsium sp.*), goldenrod (*Solidago sp.*), spirea (*Spirea sp.*) and asters (*Aster sp.*).

ARRIVAL DATES

The earliest recorded dates of the birds' spring arrival at the field during the study period were 9 April in 1965 and 1967, and 15 April in 1966. Males were singing on those dates.

Twenty-two males color-banded in 1965 were first observed in 1966 from 15 April to 13 May, and 17 color-banded males in 1967 from 9 April to 7 May. A color-banded male first seen as late as 21 May 1967 was not seen again.

In both years most of the returning males (20 out of 22 in 1966 and 16 out of 18 in 1967) arrived within a ten-day period in April (9–18 April 1966 and 15–24 April 1967.)

In 1966 and 1967, the first color-banded females were seen on 1 May and 30 April respectively. The earliest estimated start for nesting in any year was 30 April 1967. Returning color-banded females were first seen in 1966 as late as 14 June and in 1967 up to 27 May. Usually inconspicuous unless alarmed by the observer's proximity to a nest or fledgling, some females could have been in the field several weeks before being seen for the first time.

TERRITORIAL DEFENSE

Singing.—Males began singing on arrival in their territories or shortly thereafter. In all three years of the study some singing, however limited, had begun by 15 April. In two of those years the field was full of song on that date. In the third year (1965) full song came on 23 April.

Singing did not appear to be done by other than territorial males. I never heard a female sing or make any other sound other than a chip of alarm and a buzz when rejecting the advances of a male.

Songs differed from one bird to another and in one bird's repertoire, but I have no detailed notes on this. I did time one singing individual and recorded 25 songs in four minutes—an average of one song every 9.6 seconds.

Borror (1961) found that individual Savannah Sparrow songs last two to three seconds.

Several birds were usually singing by 06:00 in April. They ceased as late as 19:40 in late April, and as late as 20:20 by the end of June. Singing tapered off after 09:00 and the birds were usually still after 12:00. Singing in the evening was less than in the morning but occurred regularly. It was also less or absent in strong wind or rain.

Song was sometimes distorted by wind, making the birds difficult to hear or locate, especially when they sang from behind hummocks on the ground during pauses in foraging.

Singing decreased by mid-June, since the male stopped singing during the incubation period and did not resume until the fledglings were on their own. (He also used the perches less frequently and was less frequently seen.) When a nest was lost through predation, the male soon resumed singing.

Singing occurred mostly from perches in thistle, goldenrod and willow, and on the barbed wire fence around the field. Certain perches were used more than others.

Fighting.—The ultimate defense of Savannah Sparrow territory is a fight between males, but fights were infrequent. (No female was seen in a fight or any other defense of a territory.) Typically, the two birds rose straight up about a meter above ground and went back down, breast to breast and clawing all the way. The fights were of short duration—I never saw a rise repeated—and the birds quickly went their separate ways. I heard no sound during the fights.

Chases.—Chases by territorial males were more common than fights, especially early in the season when the territories were first established. They ceased with molt.

In all chases in which I was able to identify the pursuer, the chase was made by the territorial defender and ended at the border or shortly past it. The pursuer usually made a buzzing noise during the chase. In one instance the defender rose almost straight up about 6 meters to intercept and chase a Savannah Sparrow flying over its territory.

The pursuer often ended the chase by flying to a perch in his territory and making a chipping noise or singing. One pursuer, apparently agitated by the chase, flew from a grass clump out in his territory to a fence at the border, then back and forth two more times, singing constantly.

If the chased bird flew through more than one territory, the chase sometimes became a relay event, the first defender stopping at his border and the neighboring defender taking up the pursuit.

On three occasions a week apart in April, 1967, I saw gang chases involving as many as five or six male Savannah Sparrows. The first incident began with

a two-bird chase, the rest converging and all going down into the grass. The birds started scattering before I arrived, but I was able to identify four from their color bands. The second chase involved four birds, only one identifiable. The third incident involved five or six birds, one or two flying in from as far away as 15 meters. It broke up quickly but not before a fight occurred.

The location in all three incidents was the same "no-man's-land" between several territories. The birds identified were all territorial residents in that area. I was unable to determine if they were ganging up on a bird from outside the area—a transient, perhaps, or a new arrival—or whether a single chase between two area residents excited others into general aggression.

Border-crossings did not always end in chases, perhaps because even Savannah Sparrows have difficulty finding each other in tall grass.

On 15 May 1966, for example, a territorial male flew onto a grass tuft and, his crown feathers raised, looked around quickly in many directions but started no chase. Another Savannah Sparrow soon flushed from the base of of a nearby fence post and flew off, whereupon the first bird, his crest now down, perched quietly on the fence and no longer looked around so rapidly.

Generally, however, Savannah Sparrows stayed within their territories throughout the breeding season except when the momentum of chasing an intruder carried a male into an adjoining territory or when a parent accompanied a wandering fledgling across boundaries.

Other defenses.—Most adjustment of borders between the few territories that touched occurred without either fights or chases. Instead, the opposing males sang on either side of the line, about a meter apart, silently crowded each other back and forth across the line, or walked along the line side by side, a few centimeters apart. There were also combinations of these.

Examples:

1) M-44 was challenged at his border by another male, M-39. The birds ran side by side, occasionally buzzing and fighting. At times they were only 30 cm apart and both singing.

2) I flushed M-64, and he flew to a grassy area at his boundary. He was instantly met there by M-38 of the adjoining territory. Both then walked side by side, sometimes only centimeters apart, along their border. At one point M-64 stopped and M-38 walked on, whereupon M-64 crossed the "line." M-38 immediately rushed back at M-64 and buzzed; M-64 returned to his side and the side-by-side walking resumed. M-64 occasionally sang as he walked. After a few minutes I moved away and M-38 flew to a perch in the center of his territory and sang, ending the confrontation.

3) M-53 resisted intrusions by M-40, who had part of M-53's territory as his own the previous year. On one occasion M-40 sang from the ground in M-53's territory but was escorted back across the border. That is, M-53 flew to the ground about 30 cm from M-40 and followed M-40 as the latter walked back into his own territory. There was no audible sound.

Among encounters on fences bordering adjacent territories, one observed 12 May 1967

was typical. M-29 and M-33 approached each other, facing first one way, then another as they perched crosswise on the barbed wire. They fluttered their wings slightly, fanned their tails, raised their body feathers as if swelling, teetered forward with their heads lower than their tails, and opened their bills. At times they were only 30 cm apart.

One would back up after depressing his body feathers, while the other advanced. Then the action would be reversed. The birds see-sawed a distance of not greater than 1.5 m, more often within a one-half-to-one-meter span. All was done silently except for a few very soft buzzes.

The confrontation ended when M-33 hopped up onto a fence post a little farther away and sang. M-39 hopped down into the grass a short distance in the opposite direction and began foraging.

Other encounters on fences lacked the buzzing, wing movements and feather-raising, but the see-sawing and teetering were the same. None of the encounters resulted in fights.

Immunity from defense.—Parent birds apparently could follow their fledglings anywhere without being attacked by territorial defenders. The parents were very excitable at this stage, both birds (but particularly the male) perching closer to the observer than usual and chipping rapidly and loudly.

In June, 1966, female F-69 from an adjacent territory, possibly foraging for her nestlings, perched and chipped in M-64's territory without being chased out. But when her mate, M-18, also intruded, M-64 approached him and buzzed and M-18 retreated to his own territory.

Six days later, however, the situation changed. The nestlings had left the nest and were being tended by M-18 and F-69. The parent birds again moved into M-64's territory. Although I was unable to see whether they were following their fledglings, this time neither bird was bothered by M-64. On the contrary, M-18 approached M-64 and buzzed.

Interspecific aggression.—Aggression toward birds of other species was observed in only a few instances.

A territorial male was seen chasing a Field Sparrow (*Spizella pusilla*) which shifted only a meter or two at each rush but eventually left the territory.

A Savannah Sparrow landed beside a Song Sparrow (*Melospiza melodia*) and buzzed until the latter flew away, but in another case a Savannah Sparrow flew when approached by a Song Sparrow. In all other encounters, these two species appeared to ignore each other.

Goldfinches (*Spinus tristis*) and Bobolinks (*Dolichonyx oryzivorus*) nested in the field without being approached. On the contrary, I once saw a Bobolink chasing a Savannah Sparrow.

I saw no cases of Savannah Sparrows being aggressive toward other animals except in pursuit of insects for food.

Cessation of defense.—Nesting activity tapered off in late July, accompanied by lessening and cessation of territorial defense. The females left the study area, none being seen despite repeated inspection walks throughout all terri-

tories. The males went into molt, stopped singing and skulked through the brush. When flushed, they flew only a short distance and disappeared into the brush again. Any chipping was low in volume and not persistent. Eventually the males also left the field.

The earliest date on which molt was noticed during the study period—that is, when the males first looked ragged—was 17 July. For some males it was noticed 30 July. In all cases molt was accompanied by a cessation of territorial activity. In no case was molt seen as long as the male was still tending fledglings.

I was never able to observe molt in a female. Quite often a female would appear to be in sleek plumage while her mate looked ragged. Generally the females left earlier and may have molted during this dispersal.

The cessation of territorial defense throughout the field seemed to occur within a week's time except for a few birds still busy with nestlings or fledglings. In each of the three years there came a particular day when I noted that territorial behavior seemed to have ended. Twice it was on 25 July and once on 31 July.

DEPARTURE

The females usually left the study area within two weeks after the end of their last nest, whether the end was from predation or fledging and although both males and females tended fledglings. While they no longer defended their territories, the males stayed on as long as a month and a half, the average being about a month. By 31 July, most had gone, but a few stayed on until mid-August. One was seen as late as 10 September in 1965.

The last resident birds of 1966 were seen on 14 August. Observations in 1967 ended on 31 July, with four males and three females remaining, representing only 22 per cent of the full adult population that season. The seven birds included three pairs with late broods.

In general, the females left gradually through June and July, while most of the males left the last two weeks in July.

NATURE OF TERRITORIES

Shape.—The territories varied considerably in shape from almost square to long and rectangular and roughly triangular, with no apparent correlation between territory shape and success in attracting a mate.

Although the fields adjacent east and west were breeding areas, the Savannah Sparrows I observed generally adopted the barbed wire fences not only as much-used singing perches, but also as territorial boundaries. The birds did not cross the fences except when approached by me or for a short distance in pursuit of an intruding Savannah Sparrow. I also recorded one

instance in which a female apparently followed her fledglings into the adjacent field.

One of the two exceptions to adoption of the fences as boundaries was a Savannah Sparrow which frequently sang from a small sapling about two m beyond the fence, although the bulk of his territory was in the study field. Another bird clearly had territories which straddled the fence line in 1965 and 1967.

The fences were observed as boundaries even when they merely separated open grassland rather than being paralleled on one side by something different, such as a road, a ditch or a thicket.

Nest location.—Nests occurred anywhere in a territory, even at the border. In 1965 I discovered two nests only 2.2 m apart in adjacent territories. Both nests were successful.

Size.—Fifty-eight per cent of 62 territories marked during the three years ranged from 601 to 1200 m^2—about one-sixth to one-third of an acre. Fifteen per cent were smaller, 27 per cent larger.

The average for the 62 territories was 1,068 m^2 (0.26 acre). For the 27 territories in which no nest was found, the average size was 845 m^2; for the 35 in which nests were found it was 1,239 m^2.

The literature on the size of sparrow territories is limited. What there is indicates the Savannah Sparrows I observed had territories considerably smaller than the other species noted. I found reports of territory sizes for ten species in addition to my own figures for the Savannah Sparrow.

A comparative list follows, all figures translated into square meters:

Savannah Sparrow (*Passerculus sandwichensis*)—From 120 to 2,920 m^2, averaging 1,068 m^2 (0.26 acre). Present study.

Grasshopper Sparrow (*Ammodramus savannarum*)—4,850 to 13,330 m^2, averaging 8,200 m^2 (2.03 acres). Smith, 1963.

Baird's Sparrow (*Ammodramus bairdii*)—4,730 m^2 (1.17 acre). Cartwright, et al., 1937.

LeConte's Sparrow (*Passerherbulus caudacutus*)—1,020 to 6,300 m^2, averaging 3,320 m^2 (0.82 acre). Calculated from maps by Murray, 1967.

Henslow's Sparrow (*Passerherbulus henslowii*)—Average of 3,238 m^2 (0.80 acre). Robins, 1971.

Sharp-tailed Sparrow (*Ammospiza caudacuta*)—Female less than 4,047 m^2 (1 acre), males not territorial. Woolfenden, 1956.

Seaside Sparrow (*Ammospiza maritima*)—Nesting area, 5,830 m^2; shoreline feeding area, 4,170 m^2; total, 10,000 m^2 (2.47 acres). Woolfenden, 1956.

Tree Sparrow (*Spizella arborea*)—5,580 to 39,100 m^2 (1.38 to 9.66 acres). Heydweiller, 1935.

Chipping Sparrow (*Spizella passerina*)—4,047 to 6,070 m^2 (1 to 1.5 acre). Walkinshaw, 1944.

Field Sparrow (*Spizella pusilla*)—Less than 3,640 to 8,094 m^2 ("less than 0.9 acre" to 2 acres). Walkinshaw, 1945.

Song Sparrow (*Melospiza melodia*)—For mainland, 2,000 to 6,000 m^2 (0.5 to 1.5 acre),

Table 1
Distribution of Territories According to Size and Presence of Nests

Size (m^2)	Territories without nests	Territories with nests	Total no. of territories in size range	% of all territories	Nests found	% of territories in size range with nests
0–600	8	1	9	15	1	11
601–1200	16	20	36	58	27	56
1201–1800	1	8	9	15	12	89
1801–2400	1	4	5	8	5	80
2401–3000	1	2	3	5	2	67
Totals	27	35	62	101	47	

Nice, 1937; for lakeshore, 1,250 to 2,750 m^2 (0.31 to 0.68 acre), Suthers, 1960; for island, 160 m^2 (0.04 acre), Beer, et al., 1956.

Nest occurrence.—Fifty-four Savannah Sparrow nests were found. Behavior by adult birds indicated the probable existence of 15 more nests, for a total of 69. Thus the nests found represented about 80 per cent of those believed to have been in the field.

A breakdown of territories by size and known presence of nests is presented in Table 1. Only 47 of the 54 nests found are included. The other seven were in five territories also not included because of inadequate marking or because the nests were discovered too late to map the territories. Figure 1 shows the territories for the three years of the study.

As might be expected, most of the nests were found in the size range which also included a majority of the territories—601 to 1,200 m^2. But a comparison of the percentages of nest occurrence in the several size ranges revealed a roughly similar distribution (56 to 89 per cent) except where territories were smaller than 601 m^2. Only one of the nine territories in that range had a nest, a distribution of only 11 per cent.

Female occurrence.—The same pattern of distribution could be applied to the presence of female Savannah Sparrows in the territories. This was so because in only nine out of 45 territories in which adult females were known to be present were there no nests found, and even in eight of those nine behavior of the adult birds indicated the probable existence of nests.

It appeared, therefore, that the size of the territory had some influence on the attraction of a female, with territories larger than 600 m^2 being more attractive.

Territorial compression.—Two males experienced severe territorial compression.

In 1965, M-24 attracted a mate, F-23, to a territory originally 890 m^2 in

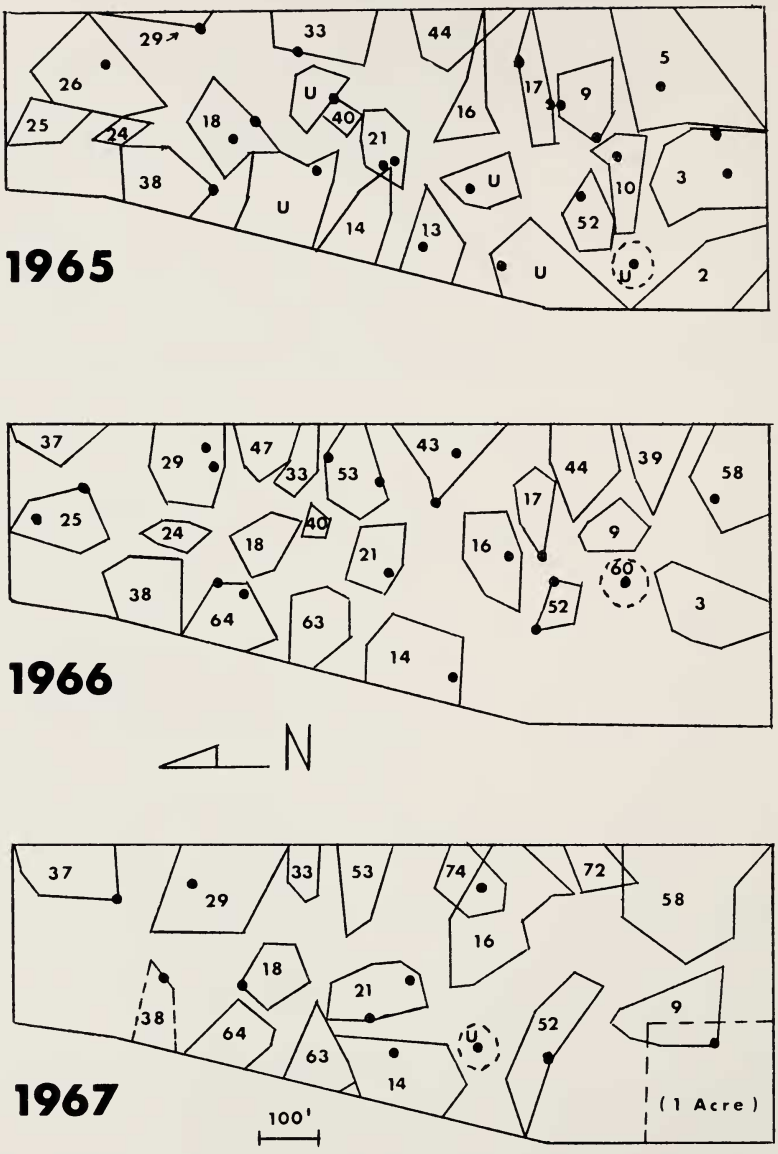

FIG. 1. Savannah Sparrow territories in field near Ann Arbor, Michigan, 1965–67. Numbers = identified males. U's = unidentified males. Dots = nests. Broken circles surround nests found too late to map territories. Broken territory at bottom, 1967—Male 38, is estimated from partial sightings.

size. Much of this was later used by another male as part of his own territory, and M-24's area shrank to 200 m^2. M-24 and F-23 apparently nested once but abandoned the field after 26 June. The following year, M-24 returned to the same spot, established a territory only 360 m^2 in size and did not mate.

The other male, M-40, first established (in 1965) a 970 m^2 territory, and F-35 became his mate. Encroachments by other males establishing adjacent territories compressed M-40's area first to 360 m^2 and then to only 200. Nevertheless, there was at least one nest and probably two. In 1966, however, M-40 returned to the same spot, established a territory only 120 m^2 in size and did not mate. He was surrounded by five other territories, the males all aggressive.

Neither M-24 nor M-40 returned to the field in 1967.

(The original sizes of their territories in 1965, before compression, are used in Table 1, since these sizes existed when the females were attracted to the areas and began nesting.)

Territorial expansion.—With the exceptions just discussed, early-arriving Savannah Sparrows did not seem consistently to claim large areas that were later scaled down by population pressure, although there sometimes was considerable border adjustment at the beginning. On the contrary, there seemed to be room between most territories for the small expansion the male frequently indulged in at the onset of a second nest.

However, I was not able to determine whether part of the old territory was abandoned so that the total area remained the same size. This was because once his territory was established, each male favored only certain perches.

Late arrivals (there were attempts to establish new territories even in July) would sometimes choose unclaimed areas between territories and attempt to crowd their way in, expanding to either side and reducing the sizes of the adjacent territories. If the unclaimed spaces were small to begin with and the attempts at expansion failed, the late arrivals were often gone the next day but sometimes stayed as long as two weeks.

Abandonment of territories.—Abandonment by one mate or the other is impossible to prove except when a missing bird shows up elsewhere. Otherwise, predation is assumed to be the cause of disappearance. During this study no males were proven to have abandoned well-established territories, although three disappeared, all in 1967. One of them had a mate, which disappeared nine days before the male and long before the usual departure time.

After having successfully reared a brood in 1966, F-69 followed her fledglings into the adjacent territory of M-64 and remained there to mate with him for a second, successful nest. Deserted M-18 spent the rest of the season singing in his own territory but did not acquire another mate. A similar occurrence was noted among Field Sparrows by Walkinshaw (1945).

Another female, F-20, disappeared after her first nest in both 1965 and 1966

with the same male, M-21, although the male remained each time. Oddly enough, after M-21's first mate of 1967 (not F-20) disappeared after laying four eggs. F-20 reappeared to mate with him again for the second nest, which was successful.

SUMMARY

Territorial behavior of Savannah Sparrows in a field in southeastern Michigan was observed for three successive breeding seasons.

Most males arrived within a 10-day period in mid-April. Females arrived over a one-month period starting at the end of April. The males established territories immediately, often returning to the same area of the field claimed in previous years.

Males defended their territories by singing from border perches, chasing intruders, walking side-by-side along the boundaries with males of adjoining territories or by assuming threatening postures face-to-face at the borders.

Birds seldom left their territories except under stress, but adults accompanying fledglings could cross boundaries with impunity.

Fifty-eight per cent of the territories ranged in size from 601 to 1,200 m^2. Fifteen per cent were smaller, 27 per cent larger. There was some enlargement between nestings.

The Savannah Sparrow territories observed were considerably smaller than those of 10 other species of sparrows reported in the literature.

The success of attracting a mate was apparently linked to territorial size, with a better chance in territories larger than 600 m^2.

Nesting activity tapered off in late July, territorial defense ended and the males molted. The females left the study area usually within two weeks after their last nests were emptied, through June and July. The males usually remained about a month after the last nests were emptied, most of them departing the last two weeks in July.

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